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THEORETICAL ARTICLE

Human Biological and Psychological Diversity

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Abstract Many evolutionary psychologists have asserted that there is a panhuman nature, a species typical psychological structure that is invariant across human populations. Although many social scientists dispute the basic assumptions of evolutionary psychology, they seem widely to agree with this hypothesis. Psychological differences among human populations (demes, ethnic groups, races) are almost always attributed to cultural and sociological forces in the relevant literatures. However, there are strong reasons to suspect that the hypothesis of a panhuman nature is incorrect. Humans migrated out of Africa at least 50,000 years ago and occupied many different ecological and climatological niches. Because of this, they evolved slightly different anatomical and physiological traits. For example, Tibetans evolved various traits that help them cope with the rigors of altitude; similarly, the Inuit evolved various traits that help them cope with the challenges of a very cold environment. It is likely that humans also evolved slightly different psychological traits as a response to different selection pressures in different environments and niches. One possible example is the high intelligence of the Ashkenazi Jewish people. Frank discussions of such differences among human groups have provoked strong ethical concerns in the past. We understand those ethical concerns and believe that it is important to address them. However, we also believe that the benefits of discussing possible human population differences outweigh the costs.

Keywords Differences · Diversity · Evolution · Genetics · Populations · Psychology · Race

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Introduction

The Arctic is a horrifically cold, often bleak, and an almost perpetually snow-covered region of the globe with long, dark winters and brief summers. During those long winters, temperatures often range between −40 and 0 °F. And yet, the Arctic is not a desolate desert of snow. Roughly 400,000 native peoples inhabit the region and have been there since well before the invention of space heaters or electric underwear. How do these people meet the exigencies of survival in such a cold, inhospitable environment?

The answer is a combination of cultural and biological adaptations. The Inuit, for example, have developed a sophisticated array of tools and weapons to facilitate survival in their harsh environment (Kelly 2013). They have learned effective ways of hunting and fishing calorie-dense animals such as seals and whales. Cultural transmission alone, however, is not responsible for the Inuit's remarkable capacity to thrive in the Arctic. They also have various physiological (and perhaps even psychological) adaptations that allow them to function in the cold, including fat insulation of vital organs, bodies with a high volume to surface area ratio, and a high basal metabolic rate which produces more body heat than other

population groups with lower basal metabolic rates (Fumagalli et al. 2015). In the relatively brief period (in evolutionary time) of roughly 30,000 years, certain populations of *Homo sapiens* in Northern Eurasia evolved *physiological* differences—perhaps best thought of as differing calibrations on existing adaptations—to the cold, which continued in the populations that entered and inhabited the Arctic (Oppenheimer 2012). The Inuit are not unique. Around the globe, a variety of human populations have thrived in disparate, often extreme climates because of both cultural ingenuity and biological adaptations (Lachance and Tishkoff 2013).

The contention that human populations possess slightly different phenotypic characteristics because of recent evolutionary pressures is not controversial. Mainstream textbooks, for example, document many instances of human biological diversity (Mielke et al. 2011; Molnar 2006). Despite this, the basics of human biological diversity are not integrated into the social sciences. Furthermore, a straightforward corollary hypothesis has remained largely unexplored in mainstream literature: that human populations also possess slightly different evolved psychological tendencies—or more specifically, calibrations on existing psychological hardware (Jensen 1998; Wade 2014). Even a standard evolutionary psychology paradigm (SEPP), a psychological research program that applies the principles of natural and sexual selection to human psychology, has asserted that there is a panhuman psychological nature, and that any nonsex-linked deviations from psychical unity among humans were likely caused by stochastic processes or pleiotropic genetic effects (Tooby and Cosmides 1990; Cosmides et al. 2003; for divergent views, see Cochran and Harpending 2009).

In this article, we make the case that there is rich human biodiversity in both morphological and psychological traits, which is a straightforward result of standard Darwinian processes acting on human populations in a wide variety of environments. Although the hypothesis that human populations possess slightly different evolved psychological traits is controversial, we contend that it is an important fact about human psychology and should not be avoided because of ethical discomfort or political sensitivities (Winegard and Winegard 2014). In fact, we think that the study of human psychological differences can promote respect and appreciation of ethnic diversity (Crow 2002). Of course, concerns about the potential political misuse of research about human diversity is understandable and reasonable (Kevles 1998). We hope that this article will encourage much needed discussion about both human differences and the moral responsibility of scientists who study it.

First, we will discuss the rate at which natural selection can create variations in animals. Common understandings aside, we will argue that natural selection can provoke change in existing adaptations quite rapidly. Then we will relate the discussion about the rate of evolution by natural selection to humans. We will argue that because modern humans migrated out of Africa at least 50,000 years ago and spread to different ecological and climatological niches, they evolved slightly different anatomical and physiological traits. We will further argue that they also evolved slightly different psychological traits and propensities (Frost 2011). Therefore, we will contend that the standard evolutionary psychology paradigm is incomplete and we will propose a different Darwinian paradigm and lay out its basic principles. Last, we will end by discussing the moral dilemmas that arise when studying and discussing human biological diversity.

Background

Before discussing human evolution and biological diversity, we will briefly discuss the SEPP, focusing specifically on its failure to appreciate adequately the breadth of human variation. After, we will examine rapid evolution, forwarding several examples of dramatic evolutionary change among nonhuman animals in very brief time spans. This will set up our discussion of human evolution and biological diversity.

The Standard Evolutionary Psychology Paradigm and Human Evolution

It is important to be clear that although there is no official statement documenting what we have called the SEPP, there does seem to be a reasonable consensus in the literature about the basic tenets of evolutionary psychology (Barkow et al. 1995; Bolhuis et al. 2011; Buller 2005; Laland and Brown 2011). Our description of the SEPP is derived from this literature but is vulnerable to complaints about oversimplification. There is, of course, substantial variation within evolutionary psychology (see, e.g., Swami 2011). Our point in covering the SEPP is not to assail what has become a foundational field of psychology. Rather, our intention is to criticize a common view of human evolution, which, we believe, is erroneous.

The SEPP arose in the late 1980s, and early 1990s, a result of the synthesis of the cognitive revolution in psychology and the "selfish gene" (or gene-centric) revolution in biology (Dawkins 1976; Pinker 1997; Plotkin 2004). According to the SEPP, human brains/minds are evolved physical systems that consist of myriad modules, or largely encapsulated processing systems that are designed to solve evolutionarily relevant and recurrent problems (Barkow et al. 1995). Human brains largely evolved in the Pleistocene, and therefore, human mental adaptations evolved to solve problems faced by distant hunter-gatherer ancestors in Africa (Buss 1995). Because evolution is a slow process, the human brain has changed only trivially since *H. sapiens* left the African continent some 100,000 years ago.

The two most important tenets of SEPP which we believe should be slightly modified are as follows (see also Bolhuis et al. 2011, box 1):

1. *Gradualism*. As we mentioned, the working assumption of the SEPP is that the human mind is comprised of complicated programs that were designed to solve recurrent evolutionary problems. Such programs require many hundreds of generations to evolve because natural selection is slow; therefore, human skulls house "stone age" minds—minds that have not been "updated" to "post-hunter gatherer conditions" (Tooby and Cosmides 2005, p. 57). We should be clear at this point and note that we are not suggesting that gradualism is, by definition, an incorrect assumption. Indeed, it has been, and should remain, a prevailing assumption among evolutionists. Rather, what we would challenge is the assumption—present in some, but not all corners of evolutionary psychology—that natural selection is precluded from working more rapidly than was previously assumed in the field of evolutionary psychology.
2. *Panhuman Nature*. The SEPP asserts that there is a universal human nature. This is a relatively straightforward consequence of gradualism, and in principle, we do not dispute it. Because evolution is a slow process, the SEPP reasoning continues, the human mind is adapted to life on the African continent, and all humans possess a universal mental architecture that has not changed in hundreds of thousands of years. Although humans did eventually leave Africa and spread across the globe, colonizing dramatically disparate environments, they have not inhabited those environments long enough to develop anything other than superficial differences from each other. The recalibration we propose in the pages to come for the concept of a panhuman nature is not that we should reject the notion of human psychological universals. Rather, we will argue that the panhuman nature possessed by our species has been differentially adjusted depending on local and regional selection pressures encountered by migrating human groups (see also, Cochran and Harpending 2009).

Rapid Evolution

The SEPP view of the pace of evolution is shared by many (though, not all) scholars. The Public Broadcasting Station's (PBS) online companion to its critically lauded series on evolution noted that, "for many species, the process (evolution by natural selection) operates so slowly that it is not observable, except over thousands or hundreds of thousands of years…" (PBS 2001).

Professors of biology often emphasize how plodding of a process natural selection is when constructing new adaptations, noting that one of the challenges to understanding it is that it requires one to imagine almost unfathomable stretches of time (Dawkins 1997). In many very important respects, *it is true that evolution is slow (or more specifically, the construction of de novo and complex adaptations requires ecological time*). Life is roughly four billion years old. Multicellular organisms are approximately 600 million years old. Mammals are some 300 million years old (Fortey 1999). The last common ancestor shared between humans and chimpanzees is roughly six million years old (Brunet et al. 2002). These are vast time scales and suggest that evolutionary change is so slow that it is difficult to understand using everyday time scales. It takes a very, very long time to arrive at a black bear from an echidna. Furthermore, there *often are* long periods of relative evolutionary stasis in which there is little evolutionary change (Dawkins 1986; see also Gould and Eldredge 1977).

Dramatic evolutionary change, however, can occur relatively rapidly; and less dramatic change, even more rapidly. Since at least the 1960s, scholars have documented sundry examples of such rapid evolution, sometimes occurring in as little as a few generations (Carroll et al. 2007). These studies demonstrate that changes in ecological and climatic conditions can induce rapid evolutionary alterations of phenotypes, though not necessarily resulting in brand new complex adaptations. Below, we will document three examples of rapid evolution, sometimes called "evolution in ecological time" (Palumbi 2002). These examples are germane to human evolution, which we will discuss in the next section, because they illustrate that novel ecological and climatic conditions, such as humans would have faced when migrating out of Africa, can spur rapid bursts of evolutionary change.

Italian Wall Lizards

In 1971, researchers transported five adult pairs of Italian wall lizards (*Podarcis sicula*) from the Croatian island of Pod Kopište to the island of Pod Mrčaru, which is roughly four and a half kilometers to the east in the Adriatic sea (Herrel et al. 2008). The islands are quite similar in elevation and terrain; however, most likely because of a larger population of sheep, the vegetation on Pod Kopište is shorter and less thick, possibly providing less shelter from aerial predators. The lizards were then allowed to live and reproduce naturally until researchers returned to examine them in the 2000s (after roughly 30 generations).

Researchers found remarkable differences between the two populations. The lizards on Pod Mrčaru, for example, are larger and have shorter hind limbs than those on Pod Kopište. Because of their shorter hind limbs, the lizards also have a slower maximum sprint speed and fatigue faster than the Pod Kopište lizards (Vervust et al. 2007). The Mrčaru lizards also exhibit an attenuated response to predators. The researchers speculated that the thicker protective brush on Pod Mrčaru caused these changes. More

specifically, the brush likely provided more safety from birds and thus eased selective pressures to maintain hypervigilant antipredator adaptations.

Researchers found other morphological differences between the populations. The head length, width, and height of the Pod Mrčaru lizards are larger than the Pod Kopište lizards; consequently, their bite force is stronger. Perhaps most remarkably, the lizards on Pod Mrčaru possess what appears to be an entirely new morphological trait (one shared with other, unrelated lizards that consume largely plant-based diets): a cecal valve—a muscle that separates the large and small intestines (Herrel et al. 2008). The valve slows down food movement and ultimately allows for the digestion of cellulose (Herrel et al. 2008). These changes may have been impelled by a shift to a more plant-based diet in the Mrčaru lizards than the ancestral population. The stronger bite force of the Mrčaru lizards probably allows them to consume smaller pieces of plants, which aids in the digestion of difficult to break down plant matter. And the cecal valve, noted above, further facilitates plant digestion.[1]

As a final point, it is imperative to consider the possibility that factors other than natural selection can explain the morphological and behavioral changes observed in the lizards. Herrel et al. (2008, p. 4794) make this point explicit, in fact: "Moreover, our data show not only rapid, directional changes in quantitative phenotypic traits related to the inclusion of plant matter into the diet, but also the evolution of novel morphological structures on extremely short time scales. Although the presence of cecal valves and large heads in hatchlings and juveniles suggests a genetic basis for these differences, further studies investigating the potential role of phenotypic plasticity and/or maternal effects in the divergence between populations are needed." In other words, when differences across groups emerge, the default assumption should not necessarily be that natural selection is responsible for shaping the divergences. Rather, that issue must be investigated empirically.

[1] It is possible that some rapid evolutionary change and/or divergence across population groups are caused by epigenetic effects rather than through the processes of natural and sexual selection (Riddihough and Zahn 2010). Epigenetics is, unfortunately, unclearly defined in much of the literature, but generally refers to information transmitted during cell division "other than the DNA sequence per se" (Feinberg and Fallin 2015, p. 1129; see also Ptashne 2013 for additional clarification regarding epigenetics). Many social scientists who use the term "epigenetics" are referring to transgenerational epigenetic effects that are induced by the external (and in particular, social) environment, and then passed transgenerationally from parent to offspring (Dickins and Rahman 2012; Moffitt and Beckley 2015). If such epigenetic effects are common, it is possible that two populations would diverge without genetic differentiation. This is an important area of future research and is currently the topic of much research, hyperbole, and debate (see, e.g., Moffitt and Beckley 2015; Ptashne 2013). We hold the possibility of epigenetic effects accounting for *some* population differences and *some* instances of rapid evolution as an open hypothesis. However, we note that the best evidence to date suggests that most epigenetic effects do not survive beyond the lifetime of an individual (i.e., they are not transgenerational) (Radford et al. 2014).

Cane Toads and Snakes

In 1935, cane toads (*Bufo marinus*) were introduced to Australia to eradicate pests that were damaging northeastern Queensland cane fields. The cane toad is a large and extremely poisonous toad with a unique cardiotoxin (Bufadienolides) (Shine 2010). Australia has no native toads; therefore, the cane toad presented a novel, poisonous prey item to many naive predators, including many species of snake (Phillips and Shine 2004, 2006). Since the early 2000s, researchers have documented intriguing instances of rapid evolution in several of these vulnerable snakes (in fewer than 23 snake generations).

Red-bellied black snakes (*Pseudechis porphyriacus*), for example, that inhabited areas exposed to cane toads evinced greater resistance to bufotoxin and decreased preference for the toad as prey relative to red-bellied black snakes not exposed (ecologically) to cane toads (i.e., tweaks on existing adaptations) (Phillips and Shine 2006). Researchers used laboratory studies to demonstrate that these changes were probably not the result of learning or of repeated exposure to bufotoxins, but were likely the result of adaptive evolutionary change. Researchers also found that several species of snakes (*P. porphyriacus* and *Dendrelaphis punctulatus*) that were exposed to toad-inhabited areas developed larger bodies and smaller relative head sizes than species not exposed to toad-inhabited areas. These adaptations appear to protect the snakes from eating large toads with fatal doses of toxin (Phillips and Shine 2004).

Yet, as we mentioned above, caution is appropriate when interpreting these findings. Regarding the possible alternative explanations to their results, Phillips and Shine (2004, p. 17154) point out that: "Although we have no direct data to distinguish between these two scenarios (selection versus plasticity), our data argue against an indirect environmental effect." Having considered the limitations of their study, the authors do contend (Phillips and Shine 2004, p. 17154): "Therefore, the morphological changes must be a consequence of (and probably also a response to) selection against small bodies and large heads.", yet they also carefully explain additional caveats and assumptions that are important to keep in mind when making such an argument (e.g., trait heritability, further response to selection, etc.). The larger point, however, is that the same type of careful inference will be required as scholars investigate similar types of research questions in human populations.

House Sparrow

As a last example, the house sparrow (*Passer domesticus*) was introduced to North America in the 1850s and quickly spread throughout the continent. In the 1960s, Johnston and Selander (1964) began to examine geographical variation in the

sparrow, documenting a wide variety of differences plausibly related to environmental and climatic diversity. For example, birds in northern environments were larger than birds in southern environments, probably because larger bodies are better able to cope with the rigors of cold winters (Johnston and Selander 1971). They also found differences in the amount of sexual dimorphism across the continent, also plausibly related to survivability in harsh winter conditions and storms (large male birds survived better than small; medium-sized female birds survived better than large or small) (Johnston and Selander 1973). Speaking of the regional variation of the house sparrow, Johnston and Selander (1964) asserted, "Racial differentiation [sic] of house sparrow populations may require no more than 50 years" (p. 548).

Summary and Consequences

As these examples illustrate, evolution by natural selection can create adaptive changes quite rapidly. In some species, these changes occurred in fewer than 20 generations (roughly the equivalent of 400 years for humans). Regional variation in North American birds is an excellent example of the power of climatic selective pressures and demonstrates the remarkable capacity of Darwinian processes to shape and tune the traits of animals. Of course, none of these examples illustrate complete morphological transformations. The path from the first reptiles to the first mammals, for example, was very long and winding (Dawkins 2005). But neither were the changes in these examples completely superficial or uninteresting to a biologist or ethologist (a general error common in previous SEPP literature).

Consider the Italian wall lizard from the first example. There is, from one perspective, a "pan-lizard" design and behavioral repertoire. Wall lizards on one island do not have entirely new behavioral patterns, do not, for example, hunt sleeping birds at night. However, the lizards on Pod Mrčaru do have *some* measurably different behavioral propensities from the lizards on Pod Kopište. If one is interested in general lizard behavioral repertoires, then it makes sense to speak of a universal Italian wall lizard nature. If, however, one is interested in the subtleties of antipredator behavioral responses, then perhaps it makes sense to speak of a differentially calibrated Italian wall lizard nature (for additional discussion and examples, see also Wada-Katsumata et al. (2013)) (see Table 1).

Human Evolution

In the next section, we will cover the basics of recent human migrations and evolution, noting that the same principles that apply to the animals we discussed above also apply to humans. We will forward several (nonpsychological) examples of regional human adaptive evolution. These examples will build the case that there are, indeed, evolutionary differences among human populations and pave the way for a further exploration of psychological differences among human populations.

Basic Overview

Anatomically, modern humans first evolved in east Africa between 200,000 and 100,000 years ago (Stringer 2012). According to some researchers, these humans were not yet cognitively modern, lacking the symbolic capacities that distinguished later humans. Klein (2009), for example, argues that humans did not cross the symbolic Rubicon until roughly 50,000 years ago. Others dispute Klein's assertion, believing that the concept of cognitive or behavioral modernity is antiquated, and should be eschewed (Shea 2011). Whatever the truth, the basic story is that *H. sapiens* evolved in east Africa around 150,000 years ago and that the archaeological record suggests an efflorescence of symbolic culture some 50,000 years ago (Klein 2009).

At some point after 150,000 years ago, humans began to migrate out of Africa. The details of these migrations are also disputed, but the basic outline is relatively uncontroversial. Sometime after 150,000 years ago, humans spread into the Near East and by about 45,000 years ago, humans had spread across much of Asia, Western Europe, Australia, and Oceania, and by roughly 15,000 years ago, they had traversed a land bridge into North America (Carto et al. 2009; Klein 2008, 2009; Stringer 2000). Some researchers contend that there were two or more waves of migrations out of Africa, with one group taking a southern route to Asia and another taking a more northerly route into Northern Eurasia and eventually into Western Europe (Reyes-Centeno et al. 2014). Others contend that there was one migration out of Africa that eventually populated the rest of the inhabited globe (Posth et al. 2016). Those who argue that there were two (or more) migrations tend to push the date of the first migration back further (~120,000 years ago) than those who contend there was just one (~60–50,000 years ago).

Whatever the granular details of the human exodus from Africa, the picture is clear enough for purposes of exploring human biological diversity. By 45,000 years ago, many human populations were reproductively isolated (by distance or by geographical obstacles such as water or mountains) from each other. And they were facing dramatically different selective regimes because they occupied radically different ecological and climatic regions of the globe (Brown 2009). In much of Europe, for example, humans encountered seasonal weather patterns, lush growing seasons punctuated by bleak and barren winters. In much of Africa, on the other hand, the weather was generally hotter and more fruitful, and the winters were much more moderate than in Europe. In fact, during

Table 1 Examples of rapid evolution in nonhuman animals

Organism	Trait(s) (altered)	Function	References
Soapberry bug (*Leptocoris tagalicus*)	Beak length (increased)	Extract seeds from balloon vine	Carroll et al. (2005)
Carolina anole (*Anolis carolinensis*)	Toepads (larger size) + lamella (greater number)	Ability to occupy higher ground due to invasion from Cuban brown lizard	Stuart et al. (2014)
Red-bellied blacksnake (*Pseudechis porphyriacus*)	Increase in body size + decrease in relative head size + increased resistance to toxin + decreased preference for cane toads as prey	Resistance to cane toad poison	Phillips and Shine (2004, 2006)
Green tree snake (*Dendrelaphis punctulatus*)	Increase in body size + decrease in relative head size	Resistance to cane toad poison	Phillips and Shine (2004)
Italian wall lizard (*Podarcis sicula*)	Increased size + decreased limb size + attenuated predator response + increased head size + increased bite strength + cecal valve	Adaptations to new island with few predators and exploitation of feeding niche involving high levels of plant matter	Herrel et al. (2008), Vervust et al. (2007)
House sparrow (*Passer domesticus*)	Morphological and color variation	Adaptation to climatic diversity	Johnston and Selander (1964, 1971, 1973)
North American red squirrel (*Tamiasciurus hudsonicus*)	Earlier seasonal breeding time	Adaptation to warming spring temperature. Allows squirrel to hoard more pinecones	Réale et al. (2003)
Domestic cat (*Felis silvestris catus*)	Human tolerance + tameness	Adaptation to human hosts allowed cat access to food supply (mice)	Driscoll et al. (2009)
Pygmy grasshopper (*Tetrix subulata*)	Melanism	Adaptive selection in response to the need to be camouflaged in recently burned environments	Forsman et al. (2011), Karpestam et al. (2013)
Mosquito (*Anopheles gambiae*)	kdr mutation allowing pyrethroid insecticide resistance	Ability to survive in agricultural locations with heavy insecticide usage	Yawson et al. (2004)
Western corn rootworm (*Diabrotica virgifera virgifera*)	Partial resistance to Cry3Bb1 maize (Bt maize)	Ability to eat transgenic Bt corn crops	Gassmann et al. (2011)
Cichlid (*Haplochromis pyrrhocephalus*)	Morphological variation + increase in gill surface area	Response to Nile perch predation and low oxygen concentrations	van Rijssel and Witte (2013), Witte et al. (2008)
Alewife (*Alosa pseudoharengus*)	Decrease in gill-raker spacing	Response to decline in large-bodied zooplankton species to feed upon	Palkovacs et al. (2014)
Ground finch (*Geospiza fortis*)	Increase in bill depth + bill length + bill width + body size	Response to drought and lack of small seeds to feed upon	Boag and Grant (1981), Weiner (1995)
Peppered moth (*Biston betularia*)	Melanism	Adaptive selection in response to darkened trees (from pollution)	Cook et al. (2012)
Trinidadian guppy (*Poecilia reticula*)	Life-history variation	Adaptive selection in response to different predators	Reznick and Endler (1982)

the last glacial maximum (~20,000 years ago), humans in much of Europe were driven into various refugia because much of the continent was cold, dry, and covered by ice (Gamble et al. 2004; Stewart and Stringer 2012). Some researchers contend that the cold, fluctuating European climate was the primary cause of the extinction of the Neanderthals (Finlayson 2005).

Humans, like many animals, actively alter their environment, which changes the selection pressures they face (Laland et al. 2001; Laland and Sterelny 2006). In fact, humans may be the paradigmatic example of a niche-creating species, using brains rather than brawn to conquer the world (Baumeister 2005; Pinker 2010). Across the globe, humans devised distinctive cultural systems to cope with their environments, creating vastly different selective regimes from one culture to another. For example, agriculture first arose in the Levant some 11,000 years ago and eventually spread across Western Eurasia (or was transmitted by conquering migrants) (Bellwood 2004). It also arose independently at different times in East Asia, Africa, and the Americas (Diamond and Bellwood 2003). Agriculture radically changed the way humans interacted with their environments, allowing them purposefully to grow several nutrient-rich crops, increasing sedentism and leading, when coupled with animal domestication, to the development of the first civilizations. The selective pressures faced by an agriculturalist are different from those faced by a hunter-gatherer—just as the selective pressures faced by a Northern European are different from those faced by a Southern African. The selective pressures faced by agriculturalists led to various adaptations that are less prevalent in populations without a history of agriculture (i.e., lifetime lactose tolerance; see Cochran and Harpending 2009). There are, in fact, myriad examples of human adaptations to specific climatic, ecological, and cultural conditions in the literature.

Skin Pigmentation

One of the most pronounced differences among human populations is the color of their skin. The average Danish person, for example, tends to have skin that is quite fair, the average Egyptian has skin that is olive, and the average Sub-Saharan African has skin that is quite dark (Jablonski 2014; Beall et al. 2010). Many researchers have suggested that skin color is adaptively tuned to ultraviolet radiation exposure and intensity (Jablonski 2004; Relethford 1997). Dark skin provides protection from potentially damaging ultraviolet radiation and became necessary after the near complete loss of hair on the human body. Excessive ultraviolet radiation penetration can cause deleterious mutations, leading to cancer, and it can also damage folate, leading to folate deficiencies (Greaves 2014; Jablonski and Chaplin 2010). Evidence supports these suggestions.

For example, Jablonski and Chaplin (2000) found robust correlations between ultraviolet radiation intensity and skin coloration, with dark, protective skin coloring found in areas exposed to concentrated ultraviolet radiation. A series of tragic natural experiments in Africa also provide support. One in every few thousand Africans is afflicted with a condition called albinism. Albinos have much lighter skin, eyes, and hair than the average person in the population. Okoro (1975), in a study of 1000 Nigerian albinos, found that many of them had potentially malignant skin cancers. Kromberg et al. (1989) found similarly elevated rates of skin cancer in albinos from South Africa. Greaves (2014) argues that this evidence supports the hypothesis that hominins developed dark skin to protect from potential ultraviolet radiation-induced cancers (but see Hong et al. 2006).

In areas exposed to less intense ultraviolet radiation, a different adaptive problem arose: the need to absorb enough sunlight to trigger pre-vitamin D_3 synthesis. Many researchers contend that this problem led to increasingly lighter skin in areas with less intense ultraviolet radiation (Greaves 2014). Some scholars argue that this explains why women have lighter skin than men in almost all known populations: Women need more vitamin D_3 because of the physiological rigors of pregnancy and lactation (Jablonski and Chaplin 2000). Others, however, contend that lighter skin may have been sexually selected in populations that were not constrained by intense ultraviolet radiation (Diamond 1994; Frost 2007). See also Darwin (1871) for a broader discussion of race and sexual selection. Either way, there is consensus that human population variation in skin color was impelled by the forces of natural (and sexual) selection and that the most conspicuous example of human biological diversity is not a side effect of genetic drift or other nonadaptive processes.

Lactose Tolerance

Another intriguing but less conspicuous example of human biological diversity is lactose tolerance/intolerance. Some human populations are able to digest milk into adulthood, whereas others are not able to. The nutrient-rich sugar in milk is lactose, which cannot be digested without the enzyme lactase. In most mammals, the production of lactase dramatically slows at an early age because they do not consume milk after weaning (Swallow 2003). Thirty-five percent of the current human population, however, is able to digest lactose into adulthood (Cochran and Harpending 2009).

Scholars contend that lactose tolerance is a remarkable example of gene-culture coevolution (Gerbault et al. 2011). In areas where agriculture and animal domestication was prevalent, humans had probably discovered ways of reducing the lactose levels of milk by fermenting it (Curry 2013). This allowed them to consume it as cheese or yogurt. But at some point, a mutation arose that allowed adults to digest lactose

(by continuing the production of lactase into adulthood), providing a new source of calories and a major fitness advantage. Geneticists estimated that humans who possessed this mutation might have produced up to 19% more offspring than those who lacked it (Bersaglieri et al. 2004). This mutation probably first emerged between the Balkans and Central Europe around 7500 years ago (Itan et al. 2009). Different mutations, which allowed adults to digest lactose, also arose among other populations across the globe (e.g., the Dinka in Southern Sudan and Maasai in Kenya and northern Tanzania) (Check 2006; Tishkoff et al. 2007). In this case of human biological diversity, the human capacity to alter ecological niches led to novel selective pressures and the spread of several genetic mutations that allowed them to survive better in an environment with milk-producing domesticates.

Altitude

As a last example of human biological diversity, consider the capacity of certain human populations, such as Tibetans, to survive the rigors of high-altitude environments. Oxygen is abundant near sea level but becomes less abundant as the air thins at higher altitudes. At 2500 m (8,50 ft) above sea level, the stresses of reduced oxygen levels become acute for humans, triggering a concatenation of physiological responses. At 4000 m (13,200 ft) above sea level, they become potentially fatal. For example, 2–6% of people exposed to altitudes over 4000 m develop a potentially mortal suite of symptoms known as high-altitude pulmonary edema (HAPE). One to 2% develop high-altitude cerebral edema (Beall et al. 2012). And yet, the Tibetan plateau, which is roughly 4500 m above sea level, is not empty. Some 600,000 people live on the plateau at altitudes exceeding 4500 m (Wu 2001).

Because they have inhabited such extreme altitudes for thousands of years, the Tibetans on the plateau possess unique high-altitude adaptations. For example, Tibetans have larger chest circumferences and greater lung capacity than Han Chinese peoples who live at lower altitudes in nearby regions (Gilbert-Kawai et al. 2014). Tibetans also breath at faster rates than other human populations, which, when coupled with their increased lung capacity, allows them to inhale large amounts of air to compensate for the reduced oxygen levels (Beall 2007). In addition, Tibetans appear to have greater blood flow than lower dwelling peoples, probably caused by a great number of vasodilators compared to vasoconstrictors than in other human populations (Beall et al. 2012). Researchers have isolated several potential genes that may be responsible for these adaptations, suggesting that the Tibetans' unique physiological profile is at least partially a product of recent natural selection (Bigham and Lee 2014; Simonson et al. 2010; Wang et al. 2011).

These examples, and many others, suggest that human populations have evolved unique physiological and anatomical profiles because of different selective pressures in disparate ecological, environmental, and climatic niches. Some of these changes, such as lactose tolerance, were impelled by cultural innovations; others, such as skin pigmentation, were compelled by climatic variation. But whatever the causes, it seems reasonable to suggest that there is some meaningful physiological variation among human population groups. Are there human races, though?

Race and Human Populations

Before proceeding with our discussion of human biological diversity, we want to discuss briefly the controversial concept of race. Thus far, we have not used the term for several reasons. Primarily, we have avoided it because it is a loaded and contentious concept, associated with a long history of prejudice and discrimination. Perhaps because of this regrettable legacy, the concept has impelled copious, often vitriolic discussion. Some philosophers and scientists have argued that race, as traditionally conceived, does not *really* exist (Kaplan and Winther 2013). It is, they contend, more of a social construct than a biological reality, a fiction foisted on the world to justify a system of racial oppression (Graves 2003). Other philosophers and scientists, however, have argued that races do exist and that the concept is as legitimate as any other fuzzy concept in biology such as cline or species (Sesardic 2010). To a large degree, the debate about race boils down to definitions (Shiao et al. 2012; Spencer 2014). One can always repudiate a particular definition of race and therefore deny that races exist.

Here, we will accept a moderate position: metaphysics aside, race is a useful concept; however, races are not immutable types, but fuzzy categories that can change depending on the level of analysis one chooses. Perhaps a useful comparison can be made between the construct of race and the construct of film category. Films are often categorized into horror, drama, comedy, and romance. These categories have some predictive value. If someone tells you that *The Karate Kid* is a coming of age drama, you have reasonable expectations about the kind of movie it is. Probably, it is not the kind of movie in which an unstoppable villain slaughters hapless teenage babysitters. Yet, these categories are not immutable, and they did not descend from a Platonic heaven. What category does *Pulp Fiction* fit in? Is it drama? Comedy? Horror? Furthermore, the usefulness and "reality" of film categories depend upon one's own interests. On Netflix, films are often sorted into remarkably narrow and precise categories such as *independent films with strong female leads*. This category is obviously more specific than comedy or horror, and it is therefore even more predictive. A movie in this list almost certainly is not about a team of action heroes who work together to defeat an

alien and a demigod. And it also almost certainly is not about a disgruntled male who joins a secret fight club. As these constructs become more and more fine grained, they become more and more predictive, but also less general and parsimonious.

The same basic principles apply to humans. Evidence from a variety of disciplines, including genetics, anthropology, archaeology, and paleontology, indicates that human populations evolved distinctive features after spreading from Africa and settling in different ecological and climatic niches (Bellwood 2013; Cavalli-Sforza et al. 1994; Molnar 2006; Wade 2014). Although such human biological variation is often ignored by social scientists, it is not really a matter of dispute among researchers in the relevant disciplines (see above). And because human populations do vary, they can be clustered and classified. The construct of race allows researchers to do this. One can begin with broad, continentally based categories: Caucasians, East Asians, Africans, Native Americans, and Australian Aborigines (Wade 2014). They are broad, general categories, but they have some predictive value. Importantly, there is nothing real in some metaphysical sense about this categorization. It is simply a pragmatic classification system that captures some differences in the world and allows researchers better to make sense of the pattern of human variation (Wade 2014). One can then move to a more granular level of categorization, replacing broad continental racial categories with more localized population categories, perhaps based on specific genetic signatures (haplotypes).

Counterarguments

There are several powerful rebuttals to the contention that race is a useful construct which we should address before proceeding. One of the most common arguments levied against the usefulness of race is that human variation is clinal or gradual, not discrete (Gravlee 2009; Hochman 2013). Consider skin color for a conspicuous example. Human populations exhibit a continuum of skin colors, not a few discrete categories. Therefore, it does not make sense to divide humans into distinct and discrete races. The charge is correct, but the target is mistaken. We are not familiar with any empirically compelling arguments suggesting that human populations are discrete (see, for example, Sarich and Miele 2005; Sesardic 2013; Wade 2014). Consider the example of film categories from above. The categories are certainly useful (which is why corporations use them), but films are not really discrete types. There is a continuum from comedy to drama (maybe measured by laughs and tears?), and it is not always clear to which particular category a film belongs. However, this does not vitiate the overall usefulness of the categories. The same applies to race. Variation is often clinal—although some population variation is relatively discrete (Risch et al. 2002; Wade 2014). But this does not mean that the categories are useless. Racial categories are fuzzy and there are often large penumbras between one category and another, but they allow researchers to capture and analyze human population variation (both phenotypically and genotypically) (Pickrell and Pritchard 2012; Rosenberg et al. 2002).

Another argument forwarded against racial classifications is that they are arbitrary. Diamond, for example, argued that "There are many different, equally valid procedures for defining races, and those different procedures yield very different classifications" (Diamond 1994, p. 84). He concludes that society (including scientists) should not codify human differences into arbitrary taxonomic groups. Such an assertion is correct. Racial classifications are not determined by essences and, therefore, can reflect the interests of the humans who are using them (Kaplan and Winther 2013). Some classification schemes might have three categories and some might have 10 and some might have 30. Furthermore, the purpose of the classificatory scheme might change the classifications. As Diamond (1994) notes, if researchers are concerned with antimalarial genes, they might develop a different classification scheme than if they are interested in skin pigmentation. However, although racial categories do not pick out real world essences, they are not as arbitrary as Diamond and others suggest.

Researchers do not concoct racial categories without motivation *just because*, and neither do they do so for purely political or social reasons. (Of course, social and political forces may interact in complicated ways with scientific narratives about reality, but that is a discussion best left to philosophers and historians of science; Roediger 2006). They are constrained by reality and by the commonly accepted principles of scientific classification, such as coherence and parsimony. Therefore, researchers generally take into account (1) evolutionary history or shared ancestry, (2) genetic profiles, and (3) phenotypic profiles when creating a classification scheme. Consider an example. One might suggest that Scandinavians should be classified with Nilo-Saharan speaking ethnic groups in East Africa because both have the ability to digest lactose into adulthood (Check 2006). But this classificatory scheme would quickly run afoul of basic parsimony. First, these groups almost certainly diverged from each other before developing the ability to digest lactose into adulthood; second, they did not evolve on the same continent; third, they do not share other phenotypic traits (such as the texture of their hair, as well as their skin pigmentation); and fourth, their ability to digest lactose appears to be caused by different genetic mutations (thus supporting the hypothesis that lactose tolerance is not a shared derived trait in these populations; Tishkoff et al. 2007). So, although racial categories are pragmatic, they are not arbitrary human inventions.

A final argument often forwarded against the use of racial classifications is that the genetic variation between human populations is small and dwarfed by the genetic variation within populations (Lewontin 1972; Templeton 2013). Therefore, so this argument goes, racial classifications contain almost no meaningful biological information. There are two counterarguments to this. First, if one focuses on the correlational structure among multiple genetic loci instead of serially examining single loci or averaging over multiple loci, then there are clear and biologically informative differences among human populations (Cochran and Harpending 2009; Edwards 2003; Tang et al. 2005). In other words, different human population groups are recognizable by their genetic profiles but only if one examines a pattern of genetic loci. Tang et al. (2005), for example, reported evidence that self-reported ethnicity corresponded very closely with genetic clusters derived from 326 microsatellite markers. Other studies have found similar power to detect accurately people's ancestry (Guo et al. 2014; Moreno-Estrada et al. 2014). Of course, this would be impossible without sufficient genetic information to distinguish among human populations.

And second, even if there were not yet clear genetic evidence of differences among human population groups, there is clear phenotypic evidence. Human populations differ from each other in many ways, both culturally and biologically, as we documented in the "Human Evolution" section. Small genetic differences can lead to noticeable and important (from a scientific point of view) phenotypic differences. Consider the Italian wall lizards from above for an example. The Pod Mrčaru lizards had, in a mere 20 generations or so, developed a novel phenotypic trait, a cecal valve, that distinguished them from their close relatives on Pod Kopište. Genetic analyses showed that both lizards belong to the same species and, in fact, are genetically indistinguishable using mitochondrial DNA (Herrel et al. 2008). Of course, there *quite likely are* genetic differences between the Pod Mrčaru and the Pod Kopište lizards. The differences, however, are difficult to detect and analyze. It would be silly to suggest that the lizards are not different simply because researchers cannot, as of now, pinpoint genetic differences between them. Of course, it is possible that future research will determine that in fact the physiological changes were not caused by genetic changes, and instead were a product of developmental plasticity. But, as of now, it is a very plausible hypothesis that they are the results of genetic changes.

Although racial categories are scientifically defensible and have been used productively (but also destructively), we prefer to use the term human population. The argument above, however, is germane whether researchers use the term race, ethnic group, breeding group, or human population. Any of these terms is a commitment to a nomenclature that accepts the reality of human biological diversity and accepts that such diversity can be classified for analytical purposes.[2]

[2] This is a slightly altered version of an argument that was made by the authors earlier (Winegard et al. 2016).

Evolutionary Differences Among Groups in Psychology

Thus far, we have introduced what we called the SEPP, and noted that we were going to recalibrate two of its basic premises. The first premise was *gradualism*, which contends that evolution by natural selection is a very slow phenomenon and that human populations have not had enough time to evolve meaningful differences. We argued that this position requires adjustment because (1) natural selection can differentially sculpt traits quite rapidly, as documented by many researchers (see "Background" section), and (2) there is copious evidence that human populations differ from each other somewhat physiologically and that natural selection continues to affect human populations (Hawks et al. 2007; Zuk 2013). Adjusting gradualism in this manner requires that we reconsider the idea of a panhuman nature. It would be remarkable, as we will discuss below, if human populations were completely similar psychologically despite having endured different selective regimes in different environments.

In this section, we will forward one approach to human diversity, contending that different human populations do indeed possess meaningfully different psychological profiles. We focus on the SEPP, but most social science approaches to human psychology accept previous conceptions of a panhuman psychological nature, so this discussion should be relevant to social scientists more broadly.

We will then forward two potential examples of human psychological diversity. These examples will be speculative, as we freely confess, because researchers have not focused on biologically based psychological differences among human populations. It is important to keep this in mind, because some of our speculations may turn out false.

Adjustment to Standard Evolutionary Psychology Paradigm

The SEPP is primarily a science of human universals. Early proponents were interested in universal mental adaptations that arose from complex organic substrates (Pinker 1997; Tooby and Cosmides 1989). And, as noted, many of the early SEPP researchers did not think there were interesting genetically based psychological differences among human populations (Cosmides et al. 2003). This approach to human nature was and is undeniably powerful and productive. From one level of analysis, the proposal of a panhuman nature is accurate and fruitful. Humans share many traits and tendencies that do not vary from population to population. Brown (1991) and other anthropologists have documented myriad human universals. Evolutionary psychologists have also explicated the mental architecture behind numerous behaviors including mating preferences, kin recognition, and the

desire for status, to name a few (Buss 1989; Henrich and Gil-White 2001; Lieberman et al. 2007).

However, as we have argued throughout this paper, there are many biologically based differences among human populations. These differences are not the result of dramatic morphological alterations. Humans on one remote island do not have three arms or two heads. Rather, they are the result of subtle, correlated changes in various organ structures. Consider an analogy that might make this clear while simultaneously illuminating the explanatory importance of population differences. Most cars are designed from the same basic blueprint and consist of similar parts—an internal combustion engine, a gas tank, a chassis, tires, bearings, spark plugs, et cetera. Cars as distinct as a Honda Civic and a Subaru Outback are built from the same basic blueprint and comprised of the same parts; so, in this sense, there is a "universal car nature" (Newton 1999). However, precise, correlated changes in these parts can dramatically change the characteristics of a car.

Humans, like cars, are built from the same basic body plan. They all have livers, lungs, kidneys, brains, arms, and legs. And these structures are built from the same basic building blocks, tissues, which are built of proteins, which are built of amino acids, et cetera. However, small changes in the structures of these building blocks can lead to important and scientifically meaningful differences in function. For example, as we noted in the "Introduction," small changes in the tissue distribution of the Inuit allow them to withstand the brutally cold winters of the Arctic. It would *literally be impossible* to answer fully the question of how the Inuit endure the Arctic or how the Tibetans survive the plateaus *without exploring these differences*—without, in other words, analyzing humans at a population level.

The human brain is the same as the human body in this regard and is not somehow immune to natural selection. Or, as Nicholas Wade (2014) succinctly noted, "brain genes do not lie in some special category exempt from natural selection. They are as much under evolutionary pressure as any other category of gene" (p. 106). It is almost certain that human populations vary psychologically in interesting, important, and scientifically meaningful ways because they were subject to different selective regimes (Rushton 1985; Wade 2007). To preview one example briefly, natural selection may have slightly dialed up the general intelligence knob on Ashkenazi Jews (i.e., an adjustment on an existing adaptation), who score roughly 110 on standardized intelligence tests (Cochran et al. 2006; Lynn 2011). Whether humans share a universal psychological profile depends upon the question one is trying to answer. If, for example, one wants to know how humans learn to recognize siblings, the concept of a panhuman psychical nature is probably fruitful (Lieberman et al. 2007). If, however, one wants to know why the Ashkenazim prosper in many societies, often despite virulent anti-Semitism, then the concept of a universal psychical profile is not only wrong, but it also positively prevents researchers from accurately answering the question (because it leads to a fruitless exploration for sociocultural causes which *cannot* be the entire story).

Because the argument that human populations vary in psychologically interesting ways is crucial for what follows, let us consider it more closely. We have noted that evolution can work quite rapidly. Lizards placed on different islands, for example, can develop slightly different responses to potential predators in only 30 or so generations (roughly 600 years for humans). We have also noted that human populations have occupied different ecological and climatic niches for many thousands of years. Last, we have noted that human populations differ from each other in many biologically interesting ways. If these three points are correct—and almost nobody would dispute them, then a nearly inescapable conclusion follows: human minds also vary among populations in interesting and meaningful ways. Why? Because cognitive and affective proclivities are every bit as crucial as anatomical and physiological structures and processes for adaptively responding to the world (including to other people). The invention of agriculture and the rise of early civilizations, for example, created selective regimes that shaped existing cognitive traits, possibly including self-control and general intelligence (Frost 2010; Frost and Harpending 2015; Rindermann et al. 2012; Wade 2014). An agricultural lifestyle might favor planning for the future and inhibiting impulses more than a hunter-gatherer lifestyle (not killing a cow today so that one can get cheese, yogurt, milk, and more meat tomorrow; Cochran and Harpending 2009). Of course, this line of speculation might be incorrect. It may turn out that agricultural societies do not reward self-control in this way. But the hypothesis is plausible, and the alternative hypothesis, namely that agricultural and hunter-gatherer lifestyles create quite similar selective regimes for cognitive and emotional traits is less plausible.

Below, we forward a couple potential examples of biologically based human population differences in psychological traits. As we warned before, these are not definitive examples. They may turn out to be entirely sociocultural in origin. However, it is plausible that they are at least partially genetically caused and, therefore, researchers should further explore them.

Self-construal Styles and Individualism/Collectivism

There are cultural/population differences in how people define themselves and their relations with others, called self-construal style (Markus and Kitayama 2010). For simplicity, one can think of self-construal as a continuum, with independent self-construal on one end and interdependent self-

construal on the other. People who have an independent self-construal tend to see themselves as autonomous, unique, and separate from other individuals, whereas people who have an interdependent self-construal style see themselves as inherently connected and enmeshed with others (Triandis 1995). These self-construal styles are associated with different cultures. Individualistic cultures are associated with independent self-construal styles; collectivist cultures are associated with interdependent self-construal styles.

Different regions and population groups tend to be associated with different construal styles and cultures. Northeast Asian cultures and peoples (China, South Korea, Japan) tend to score high on collectivism and interdependence, whereas Anglosphere cultures and peoples (Australia, Canada, New Zealand, UK, USA) score high on individualism (for some dissenting evidence and discussion, however, see also Oyserman et al. 2002). Many social scientists interpret the different construal styles as entirely cultural in origin, and they interpret the cultural differences as stemming from accidents of history (i.e., Confucianism versus Enlightenment) or geography (Nisbett 2004; Triandis 1993). In other words, most researchers in the social sciences contend that differences among human populations in construal styles are entirely environmentally caused.

However, more recent research suggests that biological differences among populations might contribute to their different cultures and construal styles. For example, Chiao and Blizinsky (2010) found a strong relation between the prevalence of a serotonin transmitter gene (*SLC6A4*) polymorphism and collectivism. Specifically, they found that populations with more carriers of the short 5-HTTLPR polymorphism were more collectivistic than populations with fewer carriers. The short 5-HTTLPR polymorphism is associated with various proclivities that, taken together, might be called emotional sensitivity, including increased negative emotion, harm avoidance, attentional biases to negative information, sensitivity to cues of rejection, and augmented risk for depression when exposed to environmental stressors (Caspi et al. 2003; Chiao and Blizinsky 2010; Karg et al. 2011; Way and Lieberman 2010; but see, Risch et al. 2009). Chiao and Blizinsky (2010) and Way and Lieberman (2010) argued that emotional sensitivity might give rise to collectivistic cultures and interdependent construal styles because collectivism creates an emotional support system that buffers sensitive phenotypes from damaging emotional stress and loneliness. Furthermore, emotional sensitivity and risk-aversion might support collectivism because people with those traits are less likely to challenge authority, assert creative ideas, or demand independence from others. (Researchers have found other polymorphisms that might explain differences between Eastern and Western cultures, but the 5-HTTLPR is a good example of this literature).[3]

If the line of argumentation above is correct, cultural differences between Northeast Asians and Western Europeans are at least partially a result of biological differences. Of course, this does not mean that culture is mechanistically determined by biology, and neither does it mean that culture does not influence cognition and behavior (Markus and Kitayama 2010). It simply means that *some* cultural differences among human populations are caused by small biological/psychological differences among those populations (Wade 2014). These cultural differences probably then reinforce the small biological/psychological differences, creating larger differences in cognitive processes (e.g., construal styles) and affective propensities (see Fig. 1). Also, once a population creates a culture, that culture can become an evolutionary selective force (denoted by the dashed and bolded arrows flowing in both directions), which augments population differences (Richerson et al. 2010).

Ashkenazi Jewish Intelligence

Psychometricians have long documented differences among populations on intelligence test scores (IQ) (Herrnstein and Murray 1994; Jensen 1998; Loehlin et al. 1975; Lynn 2015). One of the most remarkable of these differences is that Ashkenazi Jews (Jewish people from Northern and Eastern Europe and their descendants) score roughly 7–15 points (almost a full standard deviation) higher than other Europeans (Caucasians). In a review of Jewish intelligence and achievement, Lynn (2011) put the average IQ of Ashkenazi Jews at 110, which we will adopt for this article. Not only have psychometricians noted high Jewish intelligence, but other researchers have also recognized that Jewish people have obtained exceptional socioeconomic status and achieved eminence in many intellectual spheres, often despite facing centuries of ubiquitous hostility and racism (Lynn 2011; Lynn and Longley 2006; Murray 2003; Wade 2014). For just a few examples, Jews are disproportionately represented among chess grandmasters, Nobel Prize winners, Pulitzer Prize winners, and Fields Medals winners (Lynn 2011). Most social scientists have attempted to explain Jewish achievement using exclusively sociocultural (e.g., an emphasis on intellectual success and discipline) causal variables (Johnson 1988).

[3] Although this genetic research is suggestive, caution is necessary given recent evidence about the effects of single polymorphisms on complex quantitative traits. As Chabris et al. (2015) made clear when they introduced the "fourth law of behavior genetics," single alleles are likely to exert only minor effects on complex polygenic traits. The reality of the small effect of single alleles is reflected in the poor replication record of candidate gene studies, and the tendency for false positives to emerge repeatedly in research testing the effect of one gene on one behavior (Chabris et al. 2015). In the future, in might prove more fruitful to examine the distributions and frequencies of numerous trait relevant genes, not simply a handful of them.

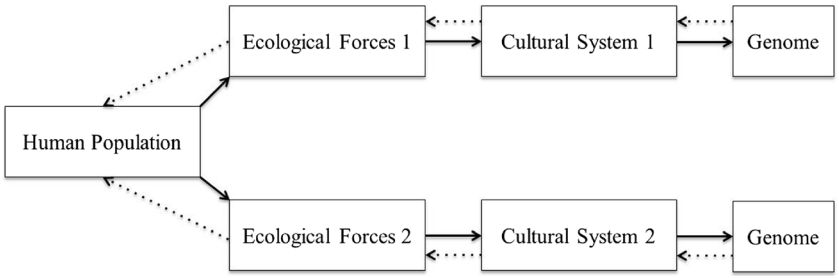

Fig. 1 Diagram of how human populations can diverge in evolutionary history. A human population first splits into two groups in different environments with different ecological and climatological forces. This creates different selective pressures on the populations (which can eventually shape their genomes, altering allele frequencies across groups). The different environments can also lead to different cultural systems, which also create different selective pressures

Recently, however, several researchers have argued that Ashkenazi Jewish intelligence is not entirely socioculturally caused, but rather is the result of unique selection pressures faced by the ancestors of modern Ashkenazi Jews (Cochran et al. 2006; Glad 2011; Lynn and Kanazawa 2008).

Cochran et al. (2006), for example, contended that because Ashkenazi Jewish people between 800 and 1700 were largely endogamous and were forced into a few, cognitively challenging occupations (e.g., accounting, money lending, and management), there were strong selective pressures on Ashkenazi Jewish intelligence. That is, because Ashkenazi Jews who were highly intelligent flourished in their limited occupational niche, they reproduced more prolifically than less intelligent Ashkenazi Jews, which ultimately led to a population level increase in intelligence. Lynn (2011) and Glad (2011) have also forwarded evolutionary accounts of Ashkenazi Jewish intelligence. Lynn's discussion is probably the most ecumenical, accepting multiple causal pathways to high Ashkenazi intelligence, including eugenic practices, occupational niche selection, and persistent persecution. Whatever the ultimate causal story, the evidence does suggest that Ashkenazi intelligence is at least partially genetically caused.

Intelligence is a highly heritable trait (a statistic that reflects genetically underpinned trait variation, and which is not to be confused with "inherited." See Sesardic (2005) for more detail). Most studies find that between 50 and 80% of within-population differences in intelligence is caused by differences in genes (Bouchard 2013; Jensen 1998; Plomin and Deary 2015). Although heritability measures cannot be uncritically applied to group differences (Block 1995), the high heritability of intelligence suggests that large group differences *might be* at least partially genetically caused (Sesardic 2005). Lynn (2011) notes that Ashkenazi Jewish intelligence scores are relatively similar wherever they are measured. Furthermore, Ashkenazi Jewish people tend to have high levels of achievement in every country they inhabit, often despite facing fierce anti-Semitism. Cochran et al. (2006) also noted that Ashkenazi Jewish people are vulnerable to a number of diseases and genetic disorders that are related to the growth of axons and dendrites and potentially to higher intelligence (Charrow 2004; Hartge et al. 1999). Many of these diseases are deleterious, so there seems to be a tradeoff between the potential for high intelligence and the risk of debilitating illness or even pre-reproductive mortality.

Of course, this evidence is not dispositive. But it is strongly suggestive. And if true, it means that at least part of the IQ gap between Ashkenazi Jews and other populations is genetic in origin. It is important to note that this does not mean that *all* of the gap can be explained by genetics. Nor does it mean that there are not sociocultural causes of Jewish intelligence and achievement (e.g., motivation for achievement; see Lynn 2011). It simply means that *some* of the intelligence differences among Ashkenazi Jews and other human populations are genetically caused as a result of natural and sexual selection.

These two examples suggest that culture is, to some degree, an extension of the human phenotypes that comprise it (Laland 2004). Small differences in biological predispositions may lead to cultural differences among human populations. Of course, this does not mean that all cultural differences are caused by subtle genetic differences. But some might be (for additional insight regarding a connected research question, see also Evans et al. 2005, as well as Mekel-Bobrov et al. 2005).

Research Program

A full integration of human biological diversity into the evolutionary social sciences will give rise to a reimagined Darwinian paradigm of research (Winegard and Winegard 2014). This certainly does not mean that the standard evolutionary psychological paradigm is otiose or needs to be completely overturned. It is not and does not. But some of its basic assumptions will have to be revised. Here, we will lay out six basic principles of this new Darwinian paradigm (see also, Boyd and Richerson 1985; Cochran and Harpending 2009; Laland et al. 2010; Lynn 2006; Rushton 1995; Wade 2014).

1. Variation is the grist for the mill of natural selection and is ubiquitous within and among human populations.

2. Evolution by natural selection has not stopped acting on human traits and has significantly shaped at least some human traits in the past 50,000 years.
3. Current hunter-gatherer groups might be slightly different from other modern human populations because of culture *and evolution by natural selection* acting to influence the relative presence, or absence, of trait-relevant alleles in those groups. Therefore, using extant hunter-gatherers as a template for a panhuman nature is problematic.
4. It is probably more accurate to say that, while much of human nature is universal, there may have been selective tuning on various aspects of human nature as our species left Africa and settled various regions of the planet (Frost 2011).
5. The human brain is subject to selective forces in the same way that other organ systems are. Natural selection does not discriminate between genes for the body and genes for the brain (Wade 2014).
6. The concept of a Pleistocene-based environment of evolutionary adaptedness (EEA) is likely unhelpful (Zuk 2013). Individual traits should be explored phylogenetically and historically. Some human traits were sculpted in the Pleistocene (or before) and have remained substantially unaltered; some, however, have been further shaped in the past 10,000 years, and some probably quite recently (Clark 2007). It remains imperative to describe what selection pressures might have been actively shaping human nature moving forward from the Pleistocene epoch, and how those ecological pressures might have differed for different human populations.

These principles lead to a number of consequences, some of which are obvious, and some of which are subtler, that are relevant to many disciplines including anthropology, criminology, economics, history, psychology, and sociology. Below, we consider a few of the most important consequences and describe what this Darwinian research program might look like.

Hunter-Gatherers and Human Nature

Although most researchers warn that hunter-gatherer peoples should *not* be treated as preserved relics of a human nature unsullied by the influences of civilization, in practice, some prior scholarship treats them exactly that way (Geher 2013; Zuk 2013). And it is very seductive to think of hunter-gatherers as more representative of human nature than people living in industrialized societies as is illustrated by the remarkable number of popular articles and books that use hunter-gatherer behavior as a guide to the essence of human nature (see, e.g., Connor 2013; De Vany 2010; Diamond 2013). From the perspective of a Darwinian paradigm based on the principles listed above, this is misguided because humans who evolved in civilizations may be slightly different, psychologically, from humans who did not (Cochran and Harpending 2009).

Equally unnecessary is the promotion of the concept of a mismatch between modern societies and "stone age" brains (Diamond 2013; Tooby and Cosmides 2005; Zuk 2013). The idea is that human brains evolved many, many thousands of years ago, but that human civilization is only roughly 4000 years old; therefore, human brains are not "designed" to deal with many of the challenges of modern civilization. Of course, the concept of mismatch is not entirely wrong. It does take time for the brain to evolve, even if the time is shorter than many researchers have presumed. So, modern food systems (fast food, processed food, readily available food) probably present unique challenges to humans who spent most of their evolutionary history in environments where calorie-rich food was reasonably difficult to obtain (Birch 1999). However, research has argued that some human populations were significantly shaped by civilization (which is most certainly true to some extent), becoming more peaceful and perhaps even more "capitalistic" during the process (Clark 2007; Frost and Harpending 2015; Wade 2014). In other words, some traits in some human populations are reasonably well attuned to many of the features of market-based civilizations.

Consequences of Ignoring Population Differences

Most social scientists steadfastly ignore human biological diversity (Boutwell et al. 2015), but if the six principles we listed are correct, this is a mistake that might impair the ability of social scientists to promote productive research programs. Consider a couple of examples.

In a meta-analysis of racial and ethnic differences in self-esteem, Twenge and Crocker (2002) found a pattern of self-esteem differences (Blacks scored higher than Whites after the 1980s and Asians scored lower than both), but ruled out, a priori, the possibility that such differences were related to biology because, according to them, "racial and ethnic categorizations are socially constructed" and are not based on "shared biological characteristics" (p. 371). This means that an entirely legitimate and plausible hypothesis about the etiology of self-esteem differences was ignored, leaving only social or cultural hypotheses. It is, of course, possible that the differences are entirely environmental in origin, but it is not certain, and ruling legitimate hypotheses out a priori on flimsy arguments (see "Race and Human Populations" section) about the nonreality of human biological diversity potentially prevents researchers from fully understanding the causes of differences in self-esteem.

In a paper on racial and ethnic differences in violent crime rates, Sampson et al. (2005) asserted that biological differences among human populations do not hold "distinct scientific credibility as causes of violence," and proceeded to adjudicate between three environment-only hypotheses about the causes of disparities in violence (p. 224). So, again, these researchers ruled out a priori a perfectly legitimate and

plausible hypothesis and proceeded to approach the data with a self-imposed theoretical limitation. Of course, it could turn out that the etiology of the disparities in crime rates is entirely environmental. But it is not really *scientific* to address the problem without carefully considering *all* potential causes dispassionately.

How the Research Program Would Work

A paradigm that accepted the reality of human biological diversity would not a priori dismiss hypotheses about biological causes for population differences; however, it would also not assume that *all* population differences are biologically caused. Population differences are, of course, caused by myriad variables and many population differences are the result of an interaction of biological, environmental, and cultural factors. Some differences, however, might be entirely cultural in origin (differences in the side of the road people drive on, or in food utensils, probably fall in this category); other differences might be almost entirely biological in origin (differences in hair texture, skin color, lactose tolerance, probably fall in this category). Because the variables that cause human population differences are often tightly intertwined and almost impossible to extricate from each other, research on the causes of group differences will be arduous, tentative, and slow. A careful description of the methodological principles of this kind of a Darwinian research program would require the length of a book, but we can highlight several of the most important.

1. The first way to approach biological variation is to look for differences among human populations. Many researchers already do this, but they almost invariably ignore the possibility that such differences are at least partially biological in origin (see Sampson et al. 2005; Twenge and Crocker 2002 for two prominent examples). To assess better human population variation, it is necessary that social scientists broaden their samples to include individuals from many societies and cultures and continue the practice of collecting data on race and ethnicity (Chiao et al. 2013; Henrich et al. 2010; Jensen 2012).
2. After researchers find examples of population differences, they should approach causal analyses neutrally. That is, researchers should not assume that population differences are sociocultural in origin; they should, instead, adopt a Bayesian approach, assuming, at a minimum equal prior probabilities for biological and sociocultural causal variables (Rowe and Rodgers 2005) and updating their beliefs on the basis of theoretical and empirical evidence. As we noted above, Twenge and Crocker (2002) should not have assumed that *only* sociocultural explanations of self-esteem differences are possible. Biological causes are possible as well, and there is no a priori reason to favor either set of explanatory variables.
3. To continue the exploration of population differences, researchers should consider a broad range of data and theory to estimate the plausibility of biological causal variables. Are there other biological differences among the populations in question? Is the trait highly heritable? Does it cohere with a pattern of differences among the groups? Consider the self-esteem example again. First, there are many biological differences among Blacks, Whites, and Asians (Molnar 2006; Rushton 1995; Sarich and Miele 2005). Second, self-esteem is at least moderately heritable (Jonassaint 2010; Neiss et al. 2006). And third, the differences in self-esteem, Blacks highest, Asians lowest, and Whites in the middle, do appear to cohere with a suite of hypothesized and known differences among the groups (Rushton 1995; Meisenberg and Woodley 2013; Minkov and Bond 2015; Templer 2008). Therefore, it may be reasonable to hypothesize that *at least* some of the differences in self-esteem among Blacks, Whites, and Asians are biologically caused (see also Boutwell et al. 2015 for an example related to antisocial behavior). Of course, this hypothesis might be disconfirmed by later exploration and analysis, but it is plausible and productive.
4. Researchers should test the posited biological cause in more depth. One should not assume, as we mentioned earlier, that differences emerging between human groups are necessarily sculpted by natural selection. Indeed, it will be difficult in many cases to confidently assert that differences are the product of directional selection and not some alternative force (e.g., genetic drift, developmental plasticity, etc.). It may also be reasonable to assume that a guiding "null hypothesis" in the absence of strong evidence (gathered from research techniques) should be that something other than natural selection—culture, developmental plasticity, etc.—is the ultimate cause of group differences.

Experiments on biological differences are difficult to conduct and are not often feasible. Yet, it is often possible to examine relevant adoption studies, cross-cultural studies, and possibly even genetic (i.e., identification of alleles or haplotypes) studies (genome-wide data becomes increasingly available for various population groups). The first two forms of studies might indicate that the putative biological variable is actually sociocultural, thus providing reasonably stringent tests of the biological hypothesis. For example, if Asians raised in homes with White parents displayed self-esteem levels equal to the White population mean, then the biological hypothesis, though not completely falsified, would lose plausibility. Or, if Asians who grew up in the USA had self-esteem levels similar to the White mean, the biological hypothesis would again lose plausibility. Genetic studies are sparse because it is difficult to isolate alleles that are correlated with

psychological traits and many such studies fail to replicate (Bosker et al. 2011; Chanock et al. 2007; Duncan and Keller 2011). But, as genetics research matures, it will provide valuable evidence for (or against) biological hypotheses.

For now, the most likely scenario is one in which the priors about causal variables gradually shift as evidence is examined and collected, but a great deal of uncertainty will remain because the evidence is not as strong as researchers would like (see Fig. 2).

One might wonder why researchers should embrace such a Darwinian paradigm given that it is unlikely to recompense them with certain knowledge about the etiology of various population differences. The answer is simple: because it will provide a fruitful research program that will shape future research and theorizing in productive ways. So, although the causal variables responsible for specific population differences may remain unknown for the foreseeable future, an honest examination of potential biological causes will spur new research and new theorizing that will produce new data. Of course, many traits are relatively the same across human populations and many of the cognitive and emotional systems researchers care about can be approached from the universalist perspective of the SEPP. Our argument is not that the SEPP is entirely wrongheaded, but just that it is unfruitful when applied to certain questions and should, therefore, be revised.

Ethical Concerns

Before concluding, we want to address the ethical concerns that have been raised about candidly studying and discussing human biological diversity. Probably, no other area of research in the social sciences has caused more fractiousness than the study of human population differences, especially the study of differences in intelligence (Hunt and Carlson 2007). Some researchers have even contended that the study of population differences is so divisive and so dangerous that scientists of good conscience should avoid it altogether (Hunt 1998; Rose 2009). Although we disagree with this advice, which we think betrays the spirit of free scientific inquiry, we do understand the concerns that arise when scientists study and candidly discuss human population differences (Ceci and Williams 2009; Gottfredson 2007). Those concerns can be addressed without stifling scientific progress or slandering researchers who decide that the study of human biological diversity is inherently interesting and worth pursuing.

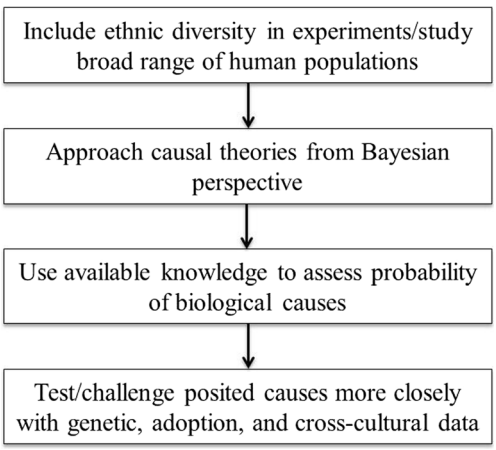
Include ethnic diversity in experiments/study broad range of human populations
Approach causal theories from Bayesian perspective
Use available knowledge to assess probability of biological causes
Test/challenge posited causes more closely with genetic, adoption, and cross-cultural data

Fig. 2 Steps for studying human biological diversity. See text for more details about each step

Contrary to the bold claims of some scientific absolutists (see, e.g., Gottfredson 2007; Kanazawa 2008), science is not an autonomous domain of intellectual activity (Connor 2005; Lewontin 1991). Science is a human social practice and is part of a larger social system. Scientific theories and knowledge have social consequences. Knowledge of the nature of subatomic particles, for example, released the devastating energy of the atomic nucleus and allowed the invention of nuclear weapons, which have threatened planetary destruction for more than 50 years. Clearly, this knowledge had dramatic ramifications and the researchers who were involved in the development of nuclear weapons carefully and cautiously reflected upon its potential consequences (Rhodes 2012). Similar concerns may apply to the study of population differences. If, for example, the dissemination of information about population differences would increase the chances of the enactment of intolerant social policies, researchers should be cautious about studying those differences and promulgating the results to the public.

There are, indeed, some potentially negative consequences of promulgating information about human population differences. However, these risks are outweighed by the potential costs of not studying and speaking responsibly about population differences. Some population differences are relatively conspicuous (skin color) and some are easily deducible (differences in intelligence, whatever the cause), which can lead to uninformed and often hateful theories as well as irresponsible and insensitive writings (see, e.g., Kersey 2012; Taylor 2011). If researchers do not responsibly study and discuss population differences, then they leave an abyss that is likely to be filled by the most extreme and hateful writings on population differences. So, although it is understandable to have concerns about the dangers of speaking and writing frankly about potential population differences, it is also important to understand the likely dangers of not doing so. It is not possible to hide the reality of human variation from the world, not possible to propagate a noble lie about human equality, and the attempt to do so leaves a vacancy for extremists to fill.

Furthermore, studying and discussing human population variation can be beneficial because it increases our knowledge about the human species, about the causes of social outcomes, and about the causes of health outcomes (Risch et al. 2002;

Tishkoff and Kidd 2004). It may be unpleasant to our moral sensibilities to discover that some human population groups have higher susceptibilities to certain diseases or to social problems in modern societies, but we cannot correct these and other problems if we do not know their etiologies. Suppose, for example, that Blacks in the USA and the UK are more likely to suffer from hypertension than Whites (Carson et al. 2011; Lane and Lip 2001). The only way we can address that problem is by sedulously studying the causes of the differences in hypertension. It might turn out that the causes are entirely environmental. But it might also turn out that Blacks have genetic profiles that make them more susceptible to hypertension than Whites. Denying the reality of this biological difference would then be positively pernicious, delaying important interventions that could ameliorate the problem. The same holds for population disparities in crime rates (Beaver et al. 2013; Jones-Webb and Wall 2008; Rushton and Templer 2009). If researchers do not carefully study the etiology of these population disparities, then they cannot fully address or propose solutions to the problem. It may be comforting to ignore such issues, but it is not beneficial to the populations involved.

If researchers responsibly educate the public about human population variation and philosophers and ethicists and politicians discuss it within a broader narrative of tolerance, the study of human population differences can not only be fruitful but also uplifting (Crow 2002). Variation is the rule in nature. No two leaves are the same. No two humans are the same. And no two human populations are the same. Instead of lamenting this, we should celebrate it just as we celebrate the rest of the vast and diverse biological world. Humans are not an exception to, but a part of, that almost endlessly variegated tapestry (Wilson 2010).

To conclude, we believe that:

1. *It does not promote the interests of society or of science to deny that human populations vary in biologically meaningful ways simply because it makes some people uncomfortable or anxious*.
2. *If some scholars deny the reality of human population variation and slander those who wish to study and discuss it openly, then extremists are likely to monopolize the conversation*.
3. *There is no reason why those who promote cultural diversity and tolerance cannot simultaneously embrace the reality of biological diversity.*
4. *Both culture-only hypotheses and genetic-based hypotheses can be dangerous when misappropriated by politicians and social theorists* (Pinker 2003). *Researchers should be cautious about forwarding any hypotheses that have potential social ramifications and should be temperate in rhetoric and humble in practice*.

Conclusion

In this article, we have argued that social scientists should integrate human biological diversity into their research programs. Specifically, we focused on the SEPP because it is probably the most successful social science paradigm to date. We contended that the SEPP is flawed because it has not fully assimilated the reality of biological diversity into its general framework (Cochran and Harpending 2009; Zuk 2013). It is important to note that some prominent researchers have attempted to do just this (e.g., Gottfredson 2002; Hart 2007; Herrnstein and Murray 1994; Lynn 2015; Meisenberg 2012). Rushton (1995), for example, forwarded an expansive account of population differences based on life-history theory. However, he was viciously attacked by many scholars (e.g., Barash 1995), and his work was quickly marginalized. Comparable fates befell other researchers who made similar suggestions. Some of these researchers, including Rushton, were probably less conciliatory than they could have been, but they nevertheless deserve recognition for important contributions to the endeavor to understand humans, and they certainly did not deserve the obloquy they received (Gottfredson 2013).

We are not naive about the obstacles a Darwinian approach to human biological diversity faces. We hope only to start a candid discussion and to forward some suggestions about how to proceed with this paradigm. Doubtless, some will continue to resist the notion that human populations differ in biologically meaningful ways. But it seems clear to us that biological diversity is the rule across the vast tapestry of life. It is true among plants, among animals, among humans, and among human populations. Instead of nervously ignoring it, we should actively celebrate it.

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